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Neighbouring-group composition and within-group relatedness drive extra-group paternity rate in the European badger (*Meles meles*)

G. ANNAVI*†‡, C. NEWMAN*, H. L. DUGDALE†§¶, C. D. BUESCHING*, Y. W. SIN*†**, T. BURKE† & D. W. MACDONALD*

*Wildlife Conservation Research Unit, Department of Zoology, Recanati-Kaplan Centre, University of Oxford, Tubney, Abingdon, Oxfordshire, UK
†NERC Biomolecular Analysis Facility, Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK
‡Biology Department, Faculty of Science, University of Putra Malaysia, Selangor Darul Ehsan, Malaysia
§Theoretical Biology, Centre for Ecological and Evolutionary Studies, University of Groningen, Groningen, The Netherlands
¶Behavioural Ecology and Self-Organization, Centre for Ecological and Evolutionary Studies, University of Groningen, Groningen, The Netherlands
**Department of Organismic and Evolutionary Biology, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA

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Abstract

Extra-group paternity (EGP) occurs commonly among group-living mammals and plays an important role in mating systems and the dynamics of sexual selection; however, socio-ecological and genetic correlates of EGP have been underexplored. We use 23 years of demographic and genetic data from a high-density European badger (*Meles meles*) population, to investigate the relationship between the rate of EGP in litters and mate availability, mate incompatibility and mate quality (heterozygosity). Relatedness between within-group assigned mothers and candidate fathers had a negative quadratic effect on EGP, whereas the number of neighbouring-group candidate fathers had a linear positive effect. We detected no effect of mean or maximum heterozygosity of within-group candidate fathers on EGP. Consequently, EGP was associated primarily with mate availability, subject to within-group genetic effects, potentially to mitigate mate incompatibility and inbreeding. In badgers, cryptic female choice, facilitated by superfecundation, superfoetation and delayed implantation, prevents males from monopolizing within-group females. This resonates with a meta-analysis in group-living mammals, which proposed that higher rates of EGP occur when within-group males cannot monopolize within-group females. In contrast to the positive meta-analytic association, however, we found that EGP associated negatively with the number of within-group assigned mothers and the number of within-group candidate fathers; potentially a strategy to counter within-group males committing infanticide. The relationship between the rate of EGP and socio-ecological or genetic factors can therefore be intricate, and the potential for cryptic female choice must be accounted for in comparative studies.

Introduction

In socially monogamous pair-breeding and group breeding species, offspring may be fathered by males from outside of the female's pair or group. This is termed extra-group or extra-pair paternity (EGP/EPP; hereafter EGP), where all, or just a proportion, of litters (broods) may have a nonresident father. EGP is a widespread phenomenon, occurring in 90% of socially monogamous bird species (Griffith *et al.*, 2002) and more than two-thirds of the 26 social group-living mammalian species investigated so far (Isvaran & Clutton-Brock, 2007; Soulsbury, 2010). EGP can play

Correspondence: Geetha Annavi, Biology Department, Faculty of Science, University of Putra Malaysia, 43400 UPM Serdang, Selangor Darul Ehsan, Malaysia. Tel.: +603 89466621; fax: +603 86567454; e-mail: geetha@upm.edu.my

an important role in the mating system and the sociogenetic structuring of otherwise socially segregated populations (Young *et al.*, 2007; Schubert *et al.*, 2011), yet there is limited understanding of the interaction between socio-ecological and genetic factors in determining the frequency of EGP (Cohas *et al.*, 2006; Isvaran & Clutton-Brock, 2007).

Although males may engage in EGP to increase breeding success (Westneat *et al.*, 1990), for example gaining kleptogamous mating opportunities despite subordinate breeding status (Young *et al.*, 2007), the advantages of EGP to females are less clear (Clutton-Brock & McAuliffe, 2009). In species where females are also able to reassess choices through cryptic mechanisms such as superfecundation, superfoetation, delayed implantation, selective implantation and embryonic re-absorption (Yamaguchi *et al.*, 2006), mating with multiple partners might have a selective advantage. For example, extra group mating combined with within-group mating might mask extra-group paternity, as a counter-strategy to infanticide (Agrell *et al.*, 1998).

Mate selection is predicated upon mixed criteria, such as: (i) which mating partners are available or accessible; (ii) mate compatibility (i.e. the rejection of unsuitable mates or unviable embryos); and (iii) mate quality (e.g. mate heterozygosity, when this is associated with increased offspring or grand-offspring fitness) (Jennions & Petrie, 2000; Kokko & Rankin, 2006; Kempenaers, 2007).

The availability of potential (candidate) partners may be an important determinant of mate selection. Mate availability is affected by the rate at which individuals encounter each other (e.g. Connor & Whitehead, 2005), the potential for female coercion (Smuts & Smuts, 1993), and the extent to which access to females might be defended by co-resident males (e.g. Treves, 1998). For example, EGP could arise if females mated randomly with whomever they encountered and, by chance, therefore mated with extra-group males (Kokko & Rankin, 2006). Under this mechanism, encounter rates between individuals from different groups will affect mating opportunities, as a function of group-range overlap or the rate of intergroup transgression. Higher encounter rates with neighbouring groups than with more isolated groups would therefore be expected to lead to higher rates of EGP with these neighbouring males.

Without further mate selection refinement (or post-copulatory selection), EGP might be nonadaptive; in fact, extra-group (or extra-pair) paternity occurs in many species without advantages being apparent (e.g. Forstmeier *et al.*, 2011). There are, however, risks associated with EGP, such as agonistic encounter with a same-sex competitor from the group (or pair) visited, or the possible rejection of extra-group young (Westneat & Stewart, 2003) if EGP can be detected. EGP can provide an adaptive tactic through which females seek to increase offspring production, for example, avoidance of infanticide when neighbouring-group/immigrant males pose a threat to infants (Agrell *et al.*, 1998; Borries *et al.*, 2011) or fertility assurance (Sheldon, 1994; Vedder *et al.*, 2011).

If social mate choice is limited, individuals might settle for a social group mate with less optimal compatibility, but mitigate this with extra group matings (Richardson *et al.*, 2005). Mate incompatibility may lead to inbreeding depression (Moore & Ali, 1984; Pusey & Wolf, 1996), and inbreeding avoidance through EGP has been shown empirically in some mammal (e.g. Sillero-Zubiri *et al.*, 1996) and bird populations (e.g. Brouwer *et al.*, 2011). Moreover, dispersing from the natal territory involves risk (Van Vuren & Armitage, 1994), with the potential to exacerbate inbreeding. EGP may therefore have evolved to mitigate inbreeding (Durrant & Hughes, 2005) as a facet of promiscuity (Brooker *et al.*, 1990), especially when offspring dispersal is delayed, or over a short distance (Pusey & Wolf, 1996). As a consequence, EGP frequency might correlate positively with the relatedness of breeding females to the mates available within their group (e.g. Kingma *et al.*, 2013).

Alternatively, the advantages of EGP for a breeding population might be due to genetic benefits, such as the 'Good-genes-as-heterozygosity Hypothesis' (Brown, 1997). This posits that 'general' allelic diversity increases fitness, consequently individuals should select mates to produce the most heterozygous offspring. The relationship between fitness and heterozygosity, however, can vary (Britten, 1996; David, 1998; Hansson & Westerberg, 2002; Coltman & Slate, 2003; Annavi *et al.*, 2014). In studies that show positive effects, heterozygosity has been associated with higher offspring survival rates (Cohas *et al.*, 2009; Mainguy *et al.*, 2009; Annavi *et al.*, 2014), breeding success (Harrison *et al.*, 2011), disease resistance (Coltman *et al.*, 1999; Whiteman *et al.*, 2006) and developmental stability (reviewed in Kempenaers, 2007). In circumstances where mate heterozygosity confers fitness benefits to offspring (Fromhage *et al.*, 2009), EGP rates would be predicted to correlate with the level of heterozygosity among within-group males (Cohas *et al.*, 2006).

European badgers (*Meles meles*) provide an informative species to address the adaptive benefits of extra-group paternity. They exhibit a variety of traits that can lead to multiple-paternity litters (Carpenter *et al.*, 2005; Dugdale *et al.*, 2007). In the study population examined here, which typifies populations in south-western England, badgers have a polygynandrous mating system (i.e. they do not have one exclusive social mate; Dugdale *et al.*, 2007, 2011); up to seven males and females breed within a social group per year, with a mean of 1.9 breeders of each sex (95% confidence interval: 1.8–2.0; range = 1–7, Dugdale *et al.*, 2007). Badgers also have low fecundity (i.e. 1–4 cubs

once per year; Macdonald & Newman, 2002; Carpenter *et al.*, 2005; Dugdale *et al.*, 2007), and extra-group paternity accounts for > 40% of offspring in our study population, which has been assigned mainly to males in neighbouring groups (Dugdale *et al.*, 2007; see also Carpenter *et al.*, 2005). An individual's social group and neighbouring groups therefore contain close relatives (Dugdale *et al.*, 2008). Badgers typically have two mating peaks, a major peak immediately post-partum and a secondary peak in the late summer/autumn (Cresswell *et al.*, 1992; see also Ahnlund, 1980). Females are induced ovulators, and gestation involves several months of embryonic diapause, where delayed implantation uncouples mating and parturition (Thom *et al.*, 2004), and then they give birth fairly synchronously around February (Yamaguchi *et al.*, 2006). Wandeler & Graf (1982) discovered that ova produced during delayed implantation may also be fertilized, resulting in superfoetation promoted by superfecundation (Yamaguchi *et al.*, 2006). This extends the opportunity for females to select the most suitable mates, through pre- and post-copulatory mate choice (Andersson & Simmons, 2006; Fisher *et al.*, 2006). Furthermore, a proportion of males extend testicular activity late into autumn – prolonging the mating season (Woodroffe & Macdonald, 1995; Buesching *et al.*, 2009). Crucially, males provide no paternal care to litters (Fell *et al.*, 2006; Dugdale *et al.*, 2010).

Badgers in this population also exhibit high group fidelity, through natal philopatry (Woodroffe *et al.*, 1995). Macdonald *et al.* (2008) report that 19% of the badgers captured at least four times in this population were found to have dispersed, mainly to adjacent neighbouring social groups. The extent to which each sex solicits extra-group mating is not known in badgers (Dugdale *et al.*, 2011). Whether within-group males actively defend their group territory and/or within-group females is highly equivocal in our study population (Stewart *et al.*, 1997; Kilshaw *et al.*, 2009). Badgers forage solitarily, and both sexes make incursions (Bohm *et al.*, 2009) and temporary visits to other groups (Macdonald *et al.*, 2008), which demonstrates that within-group males are not able to control female access to extra-group males effectively.

Based on a genetic pedigree spanning 23 years of data, here we examine the effects of local socio-ecological (breeding group size and numbers, and proportions of sexes per group) and genetic (breeding group relatedness) factors on extra-group paternity rates. We test whether EGP is more likely when there is [1a] a larger number of neighbouring-group candidate fathers (86% of EGP were assigned to neighbouring-group fathers; Dugdale *et al.*, 2007), [1b] a larger number of within-group candidate or assigned mothers and [1c] a lower number of within-group candidate fathers. We then test whether: [2a] EGP increases with the mean pairwise relatedness between within-group assigned mothers and candidate fathers, consistent with inbreeding avoidance and [2b] EGP correlates negatively with the mean or maximum heterozygosity of within-group candidate fathers (offspring first-year survival probability is positively correlated with paternal heterozygosity in years with low food availability in this population; Annavi *et al.*, 2014).

Materials and methods

Study site and field methods

This study was based on a high-density population of badgers inhabiting Wytham Woods; a 424-ha site situated 5 km north-west of Oxford, England (51°46′26 N; 1°19′19 W), which has been studied intensively since the 1970s (Kruuk, 1978a,b). A detailed description of the study site (e.g. soil, microclimates and vegetation) is provided elsewhere (Morecroft *et al.*, 1998; Savill *et al.*, 2010). At this study site, there was a mean [95% confidence interval] of 19 ([17, 21]; range = 14–26; Dugdale *et al.*, 2008) mixed-sex social groups (Johnson *et al.*, 2002; Newman *et al.*, 2011), with a mean of 13 ([12–14]; range: 2–51) individuals (including annual cubs) per social group per year (hereafter social-group-year).

Since 1987, this study has attempted to mark all individuals in the population, following a systematic capture–mark–recapture regime (Macdonald & Newman, 2002; Macdonald *et al.*, 2009). Live-trapping was conducted three to four times per annum; generally over 2 weeks in June, September and November, with 1 week of trapping in January of some years (Macdonald *et al.*, 2009). Badgers were caught in mesh-traps, baited with peanuts (Macdonald & Newman, 2002; Macdonald *et al.*, 2009), placed near the entrances of active communal badger dens, termed setts (Noonan *et al.*, 2014). Captured badgers were then transferred to holding cages and transported to a central handling facility and sedated by an intramuscular injection using ketamine hydrochloride at 0.2 mL kg^{-1} body weight (McLaren *et al.*, 2005). Upon their first capture, all badgers were tattooed with a unique number on the left inguinal region for permanent individual identification. The sex, age-class (cub or adult, based on body size and previous trapping history) and capture location (social group name) of each badger were recorded. For genetic analysis, hair samples and/or blood from the jugular vein (*ca* 3 mL) were collected from all individuals.

Social group ranges were established using a 'bait-marking' technique approximately every 2 years (Kilshaw *et al.*, 2009). The number of social group ranges within this study site has increased steadily (Macdonald *et al.*, 2004) with population density (Macdonald & Newman, 2002; Macdonald *et al.*, 2009). We defined the social group of residence of each individual per year (N = 1165; five unmarked individu-

als found dead on local roads, for which social group could not be assigned, were excluded from analyses) based on their trapping history, according to the following rules:

1 Badgers first caught as cubs (N = 839) were considered to be resident in the social group in which they were first caught (natal group; N = 709/839), unless they subsequently satisfied the dispersal rules (N = 130/839) provided by Macdonald *et al.* (2008).
2 Badgers first caught as adults (N = 326) were assigned to a social group based on the site where they were trapped most frequently (N = 273/326), unless: clear dispersal events (Macdonald *et al.*, 2008) were recorded (N = 43/326), or they exhibited equal affiliation to two social groups over their lifetime, in which case they were assigned to the social group in which they were captured initially (N = 10/326).
3 In years when females were assigned maternity, they were allocated to the social group in which their cubs were born subsequently, if this differed from the previous historical trapping data (N = 3).
4 Badger social groups often include more than one sett in their group territory and therefore territories can undergo fission, that is the splitting of a social group into two (or more) new distinct social units (da Silva *et al.*, 1993; Macdonald *et al.*, 2004), dividing the physical range occupied by the former group (defined by bait-marking). Badgers trapped in the new social group were assigned accordingly after the group split (N = 41), unless they were subsequently retrapped in the former group (N = 173).

Genotyping and parentage analysis

Details of the DNA extraction, microsatellite characterization and genotyping methods are presented elsewhere (Dugdale *et al.*, 2007; Annavi *et al.*, 2011, 2014). We genotyped 1170 individuals trapped during 1987–2010, at 35 microsatellite loci, of which 813 were cubs born between 1988 and 2010. Means are provided with their lower and upper 95% confidence values, unless otherwise stated. Mean observed heterozygosity was estimated at 0.45 [0.39, 0.51], with 4.46 [3.79, 5.13] alleles per locus. No locus, or pair of loci, departed consistently from Hardy–Weinberg equilibrium or linkage equilibrium (Annavi *et al.*, 2011). Two types of genotyping error, allelic drop-out rate (ε_1 = 0.005) and stochastic error rate (ε_2 = 0.005), were estimated using PEDANT 1.0 (Johnson & Haydon, 2007).

Parentage was determined sequentially using MasterBayes 2.47 (Hadfield *et al.*, 2006) implemented in the R statistics programme 2.12.2 (R Development Core Team, 2011) and in Colony 2.0 (Wang & Santure, 2009). For detailed description about the selection of candidate parents and their social group assignment, see Dugdale *et al.* (2007); for the MasterBayes and Colony analyses, see Annavi *et al.* (2014). We were unable to assign a mother to 16% (N = 130) of cubs and a father to 19% (N = 158).

Offspring that were fathered by males residing within their natal group in the year of conception were categorized as within-group offspring (WGO, N = 340; assigned to 125 within-group males), whereas offspring fathered by males that did not reside in their natal group were categorized as extra-group offspring (EGO, N = 315; assigned to 140 extra-group males). Cubs with unassigned paternity (N = 158) were excluded from this analysis.

Heterozygosity and pairwise relatedness

Individual standardized heterozygosity was estimated as the proportion of loci that were heterozygous, divided by the population mean heterozygosity for these loci (Coltman *et al.*, 1999) using GENHET 2.2 (Coulon, 2010) in R 2.12.2. The mean and maximum standardized heterozygosity of within-group adult males (candidate fathers) was then derived per social-group-year. Models with mean and maximum within-group candidate fathers' heterozygosity (SH) produced comparable results overall; therefore, we present results from mean SH models in the main text (see Tables S1–S4 for the results from models including maximum SH).

Pairwise relatedness values between females that were assigned maternity, and their candidate within-group mates, were estimated using Coancestry 1.0.0.1 (Wang, 2011) and averaged per social-group-year. We computed and compared two marker-based pairwise relatedness estimators, to take a comprehensive approach: the commonly used Queller and Goodnight's pairwise estimator (QG; Queller & Goodnight, 1989), and the Lynch and Ritland's pairwise estimator (LR; Lynch & Ritland, 1999), which performs well for most population compositions in simulations (Csillery *et al.*, 2006). The QG and LR pairwise relatedness estimators were highly correlated (Spearman's rank correlation coefficient = 0.91, $P < 0.001$) and yielded similar results generally. Consequently, we used the QG estimator for our main analyses (see Tables S3–S6 for the LR estimator).

Distribution of EGO and extra-group mate pairs (EGMP) across litters

We tested whether the distribution of EGO within each litter corresponded to an expected distribution, generated through binomial processes, using a chi-square goodness-of-fit test. For this analysis, we included only litters in which all cubs were assigned paternity (N = 378). The number of litters expected to include EGO was calculated as:

$$ {}_nC_X * p^X * q^{n-X} * N $$

where ${}_nC_X = n!/[(n–X)!X!]$, p = proportion of EGO in the population, $q = 1–p$, n = litter size, X = number of EGO per litter and N = number of litters of size n (Sokal & Rohlf, 1995; Perreault *et al.*, 1997). Using this formula, we also tested whether the distribution of EGMPs (each female's litter could be sired by EGMPs, within-group mate pairs (WGMPs), or both; where multiple EGMPs or WGMPs, or both a WGMP and an EGMP occurred, the litter was attributable to multiple fathers) differed from that expected under the binomial distribution.

Statistical analyses

All analyses were run in R 2.13.2 (R Development Core Team, 2011), and the rate of EGP was investigated at the litter level. We fitted generalized linear mixed models (GLMMs), using the *lmer* function with Laplace approximation in the lme4 0.999375-42 package (Bates & Sarkar, 2007).

We used two measures for EGP (expressed, throughout, as per litter): (i) the number of EGO, and (ii) the number of EGMP. We also investigated EGP from two perspectives: (i) the relative proportion of EGPs (EGO: $N_{EGO}/[N_{EGO} + N_{WGO}]$; EGMP: $N_{EGMP}/[N_{EGMP} + N_{WGMP}]$) in relation to the fixed effects, using a binomial error distribution and a logit link function, and (ii) the absolute number of EGP per litter in relation to the fixed effects by controlling for the total number of cubs (in models including EGO metrics), or the number of mate pairs involved in each litter (in models including EGMP metrics), using Poisson error structure and log link function. Here, we present results from the relative proportion models; these are compared to the absolute models, the results of which are presented in Tables S1–S6 and S8–S10.

We examined the socio-ecological effects of the number of females and males in proximity to the assigned mother, by including the following fixed effects: (i) the number of within-group assigned mothers (or within-group candidate mothers; see Tables S9–S10), (ii) the number of within-group candidate fathers, (iii) the number of neighbouring-group candidate fathers, and (iv) all two-way interactions of the three previous terms.

We included two genetic estimates of within-group candidate parents: (i) the mean (or maximum, Tables S1–S4) heterozygosity of within-group candidate fathers as a fixed effect and (ii) the mean pairwise relatedness of within-group assigned mothers and candidate fathers, as a linear and quadratic effect. To interpret main effects in the presence of interactions and quadratic effects when model averaging (Schielzeth, 2010; Grueber *et al.*, 2011), all fixed effects were standardized to a mean of zero and a standard deviation (SD) of two (Gelman, 2008). Female identity, social group and year were included as random effects in all models.

We employed an information-theoretic (IT) approach to select sets of plausible models and to estimate the overall importance of each fixed effect (Burnham *et al.*, 2011). Models were ranked by their QAICc value, such that the top model had the lowest QAICc value (Burnham *et al.*, 2011). If the difference in QAICc between the top model and the second ranked model (ΔQAICc) was ≥ 7, we considered the top model to be the only plausible model. A model's relative Akaike weight (ω) was calculated as the model's relative likelihood (exp [−0.5 * ΔQAICc]), divided by the sum of the likelihoods for all models considered (whether plausible or not).

We used the 'natural average method' (averaged over all plausible models in which the given parameter was included, weighted by the summed weights (ω) of these models; Burnham & Anderson, 2002) to estimate model-averaged parameters. Estimates of fixed effects were averaged over the plausible models, including models with and without the parameter estimates as an interaction and/or quadratic effect. Unconditional standard errors for model-averaged parameter estimates were calculated using the model.avg function in R. The relative importance of each fixed effect was calculated as the total ω of all plausible models that included the fixed effect of interest.

To investigate the rate of EGP per litter, measured as EGO and EGMP, we used an unrestricted data set that included all social-group-year data for which all trapped within-group candidate parents were genotyped, comprising 549 cubs [297 = WGO; 252 = EGO], although not all offspring were necessarily assigned both parents (unrestricted data set: no of litters = 386 [from 198 mothers]; 205 litters were assigned only to WGMP, 170 only to EGMP and 11 both WGMP + EGMP).

We also performed these same analyses using a restricted data set, including only social-group-years (as group compositions differed between years) in which all individuals were genotyped and all offspring were assigned both parents (restricted data set: no. of litters = 239 [from 147 mothers], comprising 345 cubs [174 = WGO; 171 = EGO]; 119 litters were assigned only to WGMP, 112 only to EGMP and 8 both WGMP + EGMP). The restricted data set was smaller than the unrestricted data set and thus had reduced statistical power, but including cubs that were not assigned paternity could bias the EGP rate (all within-group candidate parents were genotyped, consequently cubs that were not assigned a father were likely to be EGO). These analyses ultimately yielded very similar results to the unrestricted data set (Tables S1–S10).

Results

Patterns of EGP

Of the 502 candidate mothers and 612 candidate fathers trapped between 1987 and 2010, only 228 females (45%) and 201 males (33%) were assigned off-

spring. The mean litter size was 1.46 [1.43, 1.49] (range = 1–5). Forty-eight per cent of assigned paternities were extra-group (315 of 655 cubs), of which 85% were attributable to neighbouring-group fathers (268 of 315 cubs). EGP was detected in 64% of 225 social-group-years and 47% (178 of 378, Table 1a, Fig. 1) of litters, considering only those litters for which all offspring were assigned fathers. Of these 178 litters, 64% included one EGO (94% of them with litter size of 1), 32% included two and 4% three (Table 1a).

The number of EGO within a litter ranged from 0 to 4, with a mean of 0.65 [0.61, 0.69] in the unrestricted data set (restricted data set: 0–3, mean = 0.72 [0.67, 0.77]). Considering only litters that included EGO, 26 litters involved two fathers (16 had two extra-group fathers and 10 had one extra-group and one within-group father). No litters were fathered by more than two extra-group males. The remaining 152 litters were fathered exclusively by one extra-group male (Table 1b).

The number of assigned EGMP per litter ranged from 0 to 2 with a mean of 0.51 [0.48, 0.54] in the unrestricted data (restricted data set: 0–2, mean = 0.54 [0.50, 0.58]). EGO were not distributed evenly among litters: attributing a probability of 0.48 (the mean population EGP rate) to each offspring being assigned as EGO, we observed significant differences in the number of EGO according to litter sizes (per assigned mother, per social-group-year) than expected, according to the binomial probability distribution ($\chi^2 = 75.25$, d.f. = 13, $P < 0.001$, Table 1a). The number of EGMP within a litter had a random distribution ($\chi^2 = 5.54$, d.f. = 4, $P = 0.236$, Table 1b). Sixty-four per cent of females (unrestricted data set; 65% in restricted data set) mated with an extra-group male during their lifetime, with a maximum of five and a mode of one different mating partner pairs.

Table 1 Distribution of (a) extra-group offspring (EGO) and (b) extra-group mate pairs (EGMP) within litters that include only cubs that had both parents assigned. The numbers of litters expected from binomial probabilities are shown in parentheses.

Litter Size	No. of EGO per litter					Total litters
	0	1	2	3	4	
(a)						
1	132 (129.1)	107 (109.9)	–	–	–	239
2	57 (34.1)	6 (58.1)	54 (24.8)	–	–	117
3	10 (3.2)	1 (8.0)	2 (6.9)	7 (1.9)	–	20
4	1 (0.2)	0 (0.6)	1 (0.7)	0 (0.4)	0 (0.1)	2
Total	200 (166.6)	114 (176.6)	57 (32.4)	7 (2.3)	0 (0.1)	378

Number of mates	No. of EGMP per litter			Total litters
	0	1	2	
(b)				
1	188 (180.2)	152 (159.8)	-	340
2	12 (10.7)	10 (18.9)	16 (8.4)	38
Total	200 (190.9)	162 (178.7)	16 (8.4)	378

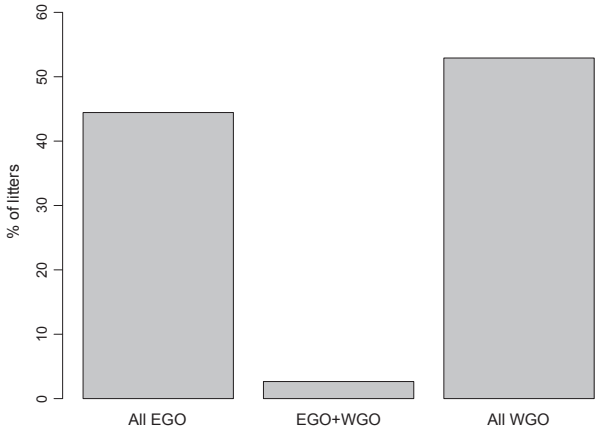

Fig. 1 Percentage of litters with only within-group offspring (WGO), only extra-group offspring (EGO) and having both WGO and EGO. Data were restricted to litters that include only cubs with both parents assigned ($N = 378$). Values at the top of each bar represent the numbers of offspring.

Socio-ecological effects of breeding group size

The number of neighbouring-group candidate fathers had a positive effect on both the absolute number and relative proportion of EGP (measured as EGO or EGMP per litter), with both the unrestricted and restricted data sets (Table 2, Fig. 2, Tables S7 and S8 and Fig. S1). Higher numbers of within-group candidate fathers were associated with a lower proportion of EGO and EGMP per litter (Table 2); this ceased to be the case, however, when litters with incomplete paternity assignment were excluded, showing that this effect differs when restricted data are used (Table S7). We also found no associations between the number of within-group candidate fathers and the absolute numbers of EGO and EGMP (Table S8).

A higher number of assigned mothers in the natal group was associated with lower relative proportions of EGO and EGMP per litter (Table 2), when using the unrestricted data set. Using the restricted data set, this effect was only detected in the EGO analysis (Table S7). Models that included candidate mothers, rather than assigned mothers, yielded similar results overall; however, the number of candidate mothers was not significant in the restricted analyses of the relative proportion of EGO and EGMP (Tables S9 and S10).

Genetic factors

The mean pairwise relatedness between within-group assigned mothers and candidate fathers was associated positively with both the relative proportion and abso-

Table 2 Model-averaged parameter estimates over all submodels with ΔAICc< 7, testing the relative proportion of extra-group offspring (EGO) and extra-group mate pairs (EGMP) in a litter in relation to local group density and composition using the unrestricted data set. WGO = within-group offspring. M = No. of within-group assigned mothers. WGCF = No. of within-group candidate fathers. NGCF = No. of neighbouring-group candidate fathers. Mean SH = Mean standardized heterozygosity of within-group candidate fathers. QG = Queller and Goodnight's mean pairwise relatedness estimator between within-group assigned mothers and candidate fathers. QG^2 = quadratic effect of QG. * = Interaction term. REML = Restricted maximum likelihood. All fixed effects were standardized to a mean of zero and a standard deviation of two. Bold estimates have a confidence interval that does not overlap with zero.

	The relative proportion of EGO				The relative proportion of EGMP			
Explanatory variable	Estimate	Unconditional SE	95% Confidence Interval	Relative importance	Estimate	Unconditional SE	95% Confidence Interval	Relative importance
(Intercept)	0.37	0.41	(−0.43, 1.18)	–	0.14	0.29	(−0.43, 0.70)	
Mean SH	−0.74	0.42	(−1.56, 0.08)	0.57	−0.44	0.34	(−1.11, 0.24)	0.42
WGCF	**−1.04**	**0.44**	**(−1.90, −0.18)**	**0.94**	**−0.87**	**0.35**	**(−1.56, −0.18)**	**0.94**
M	**−0.98**	**0.35**	**(−1.66, −0.3)**	**0.98**	**−0.61**	**0.30**	**(−1.19, −0.03)**	**0.90**
NGCF	**1.34**	**0.48**	**(0.41, 2.28)**	**1.00**	**1.18**	**0.37**	**(0.46, 1.91)**	**1.00**
QG	**1.51**	**0.49**	**(0.55, 2.48)**	**0.98**	**1.19**	**0.37**	**(0.47, 1.90)**	**1.00**
QG^2	**−1.65**	**0.66**	**(−2.93, −0.36)**	**1.00**	**−1.04**	**0.51**	**(−2.04, −0.05)**	**0.73**
M*WGCF	1.08	0.73	(−0.35, 2.51)	0.44	0.70	0.65	(−0.56, 1.97)	0.32
M*NGCF	0.85	0.68	(−0.49, 2.19)	0.33	0.94	0.58	(−0.20, 2.07)	0.49
WGCF*NGCF	−0.87	0.84	(−2.52, 0.78)	0.41	−0.74	0.68	(−2.07, 0.59)	0.35

Full models:
Model EGO
y < – cbind(EGO,WGO)
Model < – lmer (y ~ Litter Size + (1|Year) + (1|Social Group) + (1|Mother ID) + M + WGCF + NGCF + Mean SH + QG + QG^2 + M*WGCF + M*NGCF + WGCF*NGCF, family=binomial, REML = FALSE, data=Unrestricted)
Model EGMP
y < – cbind (EGMP, WGMP)
Model < – lmer (y ~ Number of mates + (1|Year) + (1|Social Group) + (1|Mother ID) + M + WGCF + NGCF + Mean SH + QG + QG^2 + M*WGCF + M*NGCF + WGCF*NGCF, family=binomial, REML = FALSE, data=Unrestricted).

lute number of EGP across litters (Tables 2, S7 and S8). We observed a negative quadratic effect of pairwise relatedness on the absolute number of EGO (but not on EGMP; Fig. S2 and Table S8A) and the relative proportion of EGO and EGMP per litter (Fig. 3 and Table 2). This quadratic relationship remained significant even after exclusion of the two outliers. There was no quadratic relationship, but a positive first-order association in the restricted data set (Tables S7 and S8B). The mean heterozygosity of within-group candidate fathers was not associated with either the absolute or relative proportion of EGP (Tables 2 and S7–S8).

Discussion

In reality, sexual selection is not predicated upon free choice (Millstein, 2002; Walsh *et al.*, 2002). Although mate selection may relate to perceived quality and compatibility, with realized offspring further honed by post-copulatory mechanisms, the actual availability of mates is also a major contributing factor (Eshel, 1979; Clutton-Brock & McAuliffe, 2009). Capacity to access mates may simply be determined by encounter rate, or it may be limited (actively or passively). Furthermore, although females are typically the choosy sex (Clutton-Brock & McAuliffe, 2009), males can also exhibit prudence (Wedell *et al.*, 2002), and intermale or interfemale competition can restrict free access to mating partners (Preston *et al.*, 2003). As a consequence, ecological, sociological and genetic factors interact to constrain the pace of evolution (Emlen & Oring, 1977).

Extra-group (or extra-pair) copulation is well documented in birds (e.g. Schwartz *et al.*, 1999; Pryke *et al.*, 2010) and mammals (e.g. Cohas *et al.*, 2006). We observed that 48% of offspring in this badger population were assigned extra-group fathers, and the majority of EGP (85%) were attributed to candidate fathers from neighbouring groups. This demonstrates that the social group unit does not correspond to a breeding unit (Carpenter *et al.*, 2005; Dugdale *et al.*, 2007). We also showed that the rate of EGP was associated with the number of each sex in each group, as well as genetic parameters.

Socio-ecological factors

We found that, when the number of candidate males in neighbouring groups was greater, there was a higher rate of EGP. Furthermore, when the number of within-group candidate fathers and also within-group candidate or assigned mothers was higher, the relative proportions, but not the absolute numbers, of both EGO

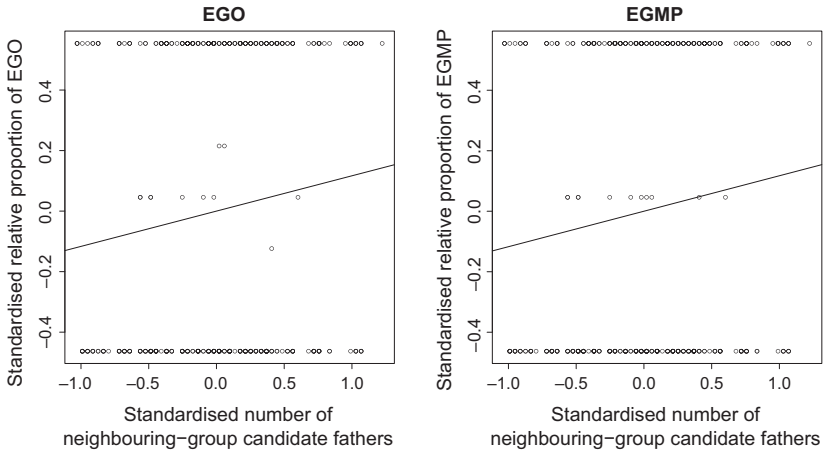

Fig. 2 The relationship between the number of neighbouring-group candidate fathers and the relative proportion of extra-group paternity (EGP) measured as extra-group offspring (EGO) and extra-group mate-pairs (EGMP) per litter using the unrestricted data set. Data points represent the standardized (mean of zero and a standard deviation of two) raw data from which the regression lines are derived.

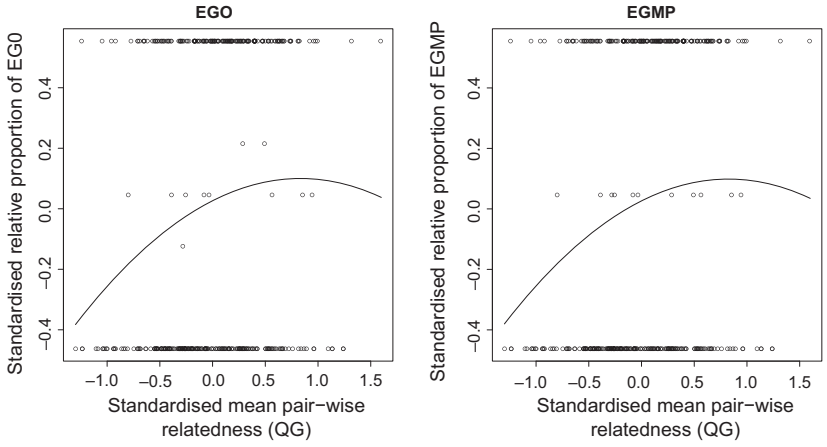

Fig. 3 The relationship between the mean pairwise relatedness (Queller and Goodnight's estimator) of assigned mothers and candidate fathers within each social-group-year, and the relative proportion of extra-group paternity (EGP) measured as extra-group offspring (EGO) and extra-group mate pairs (EGMP) per litter using the unrestricted data set. Data points represent the standardized (mean of zero and a standard deviation of two) raw data from which the regression lines are derived.

and EGMP per litter were lower in the unrestricted, but generally not in the restricted, analyses. That the rates of EGO and EGMP were lower in the unrestricted analyses probably arose because cubs with unassigned parents were present in these groups (which were likely to be extra-group parents, because both analyses only included groups in which all resident candidate parents were genotyped); however, including these groups added statistical power to the analyses. The smaller sample size of the restricted data set produced effects in the same direction, but the 95% confidence intervals around these estimates overlapped zero.

The largest socio-ecological model-averaged parameter estimate was attributed to the number of neighbouring-group males (Tables 2 and S7–S8). The number of within-group candidate fathers and candidate/assigned mothers, however, also affected the rate of EGP. The lower rate of EGP in groups with more within-group candidate fathers might be a tactic to deter within-group males from killing EGO. In contrast, females could use EGP as a counter-strategy to infanticide committed by extra-group males (Agrell *et al.*, 1998).

Our finding of lower EGP with greater numbers of candidate/assigned mothers in a group is in contrast to Isvaran & Clutton-Brock (2007). Their meta-analysis of 26 mammal species found that higher rates of EGP were associated with larger numbers of within-group females and that lower rates of EGP occurred in species with longer mating seasons. They concluded that within-group males are less able to mate guard when more within-group females are present and when the breeding season is extended. Following a post-partum mating peak in February/March, badgers can continue to mate throughout the summer, occasionally up until December, yet 48% of cubs were EGO. There is little evidence that male badgers mate guard; rather, non-competitive serial copulations with different partners underscore a freely promiscuous system (Dugdale *et al.*, 2007). Moreover, female badgers are able to reject matings (Dugdale *et al.*, 2010), preventing individual males from monopolizing females. Delayed and selective implantation, superfoetation and superfecundation then facilitate cryptic female choice, which should be accounted for in meta-analyses.

In socially paired species, the constraints of limited social mate choice, due to a lack of breeding territories, will lead to unpaired females pairing with any available unpaired male possessing a breeding territory (Richardson *et al.*, 2005). In this high-density badger population, contact occurs frequently between groups (Macdonald *et al.*, 2008) comprising multiple (breeding) males and females (Dugdale *et al.*, 2007, 2008). Females mate promiscuously (Dugdale *et al.*, 2011) and delayed implantation allows them to mate whenever a male is available (Yamaguchi *et al.*, 2006), thus females are unlikely to be constrained by the availability of mating partners. Furthermore, we have found no evidence for clear mating hierarchies in these badgers; that is, male mounting frequency is not related to dominance rank or body condition index, and male mounting frequency does not correlate with paternity success (Dugdale *et al.*, 2011).

If females mate indiscriminately with whomever they encounter, and thus by chance mate with extra-group males (Kokko & Rankin, 2006), then EGP would not necessarily be adaptive. Nevertheless, the correlation we observed with relatedness precludes parentage from being totally random. When the relative proportion of neighbouring-group candidate fathers was higher, the rate of EGP was greater. We assume that greater neighbouring-group mate availability implies a greater likelihood of contact. This type of mating system could be due to nonexclusive use of feeding ranges (Stewart *et al.*, 1997) or facilitated by the relatively high rate of temporary intergroup movements observed in this population, even from a maximum of just four trapping events per year (see Macdonald *et al.*, 2008; Huck *et al.*, 2008; see also Stewart *et al.*, 1997). These visits might serve to ingratiate males with females in adjacent groups and exploit EGMP encounter rate, to broaden mate selection options. Encounter rate-based mating could arise if the genetic basis of a female's response to her social mate (within-group males) and extra-group males is the same (Within-sex Genetic Correlation Hypothesis; Forstmeier *et al.*, 2011). Alleles for resistance to (group-) infidelity may, however, also convey resistance to (group-) fidelitous copulations, leading to infertility (Arnqvist & Kirkpatrick, 2005).

Genetic factors

We found no evidence that badgers were seeking heterozygosity in their within-group mating partners (heterozygous advantage; Jennions & Petrie, 2000), although we did not test for an environmental interaction. The propensity for males and females to engage in promiscuous mating may be affected by the same set of alleles (Halliday & Arnold, 1987). There is likely to be strong positive selection for alleles that enhance promiscuous behaviour in males (Albrecht *et al.*, 2007). If promiscuous behaviour is heritable (Reid *et al.*, 2011), pleiotropic effects on these sexually selected alleles could also cause promiscuous behaviour to evolve in females, despite antagonistic selection (Rice, 1992) known as the between-sex genetic correlation hypothesis (Halliday & Arnold, 1987; Forstmeier *et al.*, 2011).

The mean pairwise relatedness between within-group assigned mothers and candidate fathers had high relative importance, for both the relative proportion and the absolute number of EGP (Tables 2 and S7 and S8). The rate of EGP increased with greater relatedness between within-group assigned mothers and candidate fathers, showing a negative quadratic effect such that the rate of EGP plateaued with high relatedness. Small sample size, however, prevented us from testing this effect (Fig. 3).

Female preference for immigrant males over residents, when the residents are relatives, is theoretically predicted to occur when inbreeding is costly (Lehmann & Perrin, 2003). Badgers might avoid inbreeding; Annavi *et al.* (2014) report positive correlations between offspring first-year survival probability and paternal heterozygosity in this same population in summers with a good food supply (from the proxy of wet conditions, yielding abundant earthworm food). Additionally, assigned within-group parent pairs in this population were less related than randomly assigned within-group pairs (Sin, 2012), but simulations including all potential parent pairs are required to determine whether inbreeding avoidance occurs. Intergroup promiscuity, facilitated by frequent temporary visits between groups (Macdonald *et al.*, 2008), seems a plausible mechanism to avoid inbreeding, circumventing the need for permanent dispersal, and the associated risks.

Conclusions

Studies of the ecological correlates of EGP in mammals have focused on the spatial and temporal grouping of females and males within groups (Isvaran & Clutton-Brock, 2007). We highlight that the number of neighbouring males is an important and overlooked parameter, along with the potential for cryptic female choice. From the combined socio-ecological and genetic correlates of EGP in badgers, it is possible that the genetic effects we observed could occur through cryptic female choice, superimposed on a backcloth of random mating. Further research is required to elucidate the costs and benefits of EGP in mammals; for example, the survival, recruitment or life-time reproductive success of WGO versus EGO, and whether there is a genetic basis to EGP.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 The relationship between the number of neighbouring-group candidate fathers and the mean absolute number of extra-group paternity (EGP) measured as extra-group offspring (EGO) and extra-group mate-pairs (EGMP) per litter using the unrestricted data set.

Figure S2 The relationship between the mean pairwise relatedness (Queller and Goodnight's estimator) of assigned mothers and candidate fathers within each social-group-year, and the mean absolute number of extra-group paternity (EGP) measured as extra-group offspring (EGO) and extra-group mate-pairs (EGMP) per litter using the unrestricted data set.

Table S1 Model-averaged parameter estimates over all sub-models with ΔAICc < 7, testing the relative proportion and absolute number of extra-group offspring (EGO) in a litter in relation to local group density and composition.

Table S2 Model-averaged parameter estimates over all sub-models with ΔAICc < 7, testing the relative proportion and absolute number of extra-group mate-pairs (EGMP) in a litter in relation to local group density and composition.

Table S3 Model-averaged parameter estimates over all sub-models with ΔAICc < 7, testing the relative proportion and absolute number of extra-group offspring (EGO) in a litter in relation to local group density and composition.

Table S4 Model-averaged parameter estimates over all sub-models with ΔAICc < 7, testing the relative proportion and absolute number of extra-group mate-pairs (EGMP) in a litter in relation to local group density and composition.

Table S5 Model-averaged parameter estimates over all sub-models with ΔAICc < 7, testing the relative proportion and absolute number of extra-group offspring (EGO) in a litter in relation to local group density and composition.

Table S6 Model-averaged parameter estimates over all sub-models with ΔAICc < 7, testing the relative proportion and absolute number of extra-group mate-pairs (EGMP) in a litter in relation to local group density and composition.

Table S7 Model-averaged parameter estimates over all submodels with ΔAICc < 7, testing the relative proportion of extragroup offspring (EGO) and extra-group mate-pairs (EGMP) in a litter in relation to local group density and composition using the restricted data set.

Table S8 Model-averaged parameter estimates over all submodels with ΔAICc < 7, testing the absolute number of extra-group offspring (EGO) and extra-group mate-pairs (EGMP) in a litter in relation to local group density and composition using the (A) unrestricted and (B) restricted data set.

Table S9 Model-averaged parameter estimates over all sub-models with ΔAICc < 7, testing the relative proportion and absolute number of extra-group offspring (EGO) in a litter in relation to local group density and composition.

Table S10 Model-averaged parameter estimates over all sub-models with ΔAICc < 7, testing the relative proportion and absolute number of extra-group mate-pairs (EGMP) in a litter in relation to local group density and composition.

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